ICES CM 2004/L:02

A new retention index for the central Baltic Sea: long-term hydrodynamic modelling used to study recruitment variability in central Baltic sprat, *Sprattus sprattus*

Hannes Baumann[1]*, Hans-Harald Hinrichsen[2], Fritz Köster[3], and Axel Temming[1]

[1]*Corresponding author: Institute of Hydrobiology and Fisheries Science, Olbersweg 24, 22767, Hamburg, Germany [tel: +49(0)40 42838 6616, fax: +49(0)40-42838 6618, e-mail: hannes.baumann@uni-hamburg.de].

[2] IfM-Geomar, Düsternbrooker Weg 20, 24105, Kiel, Germany

[3] Danish Institute for Fisheries Research, Charlottenlund

Keywords: long-term hydrodynamic modelling, Lagrangian drifters, retention, dispersion, sprat recruitment, central Baltic Sea

Abstract

To study inter-annual differences in drift patterns of larval sprat from the Bornholm Basin, we used a 3D, eddy-resolving circulation model of the Baltic Sea and simulated the drift of Lagrangian particles for each of 24 years (1979-2002) of available forcing data. We observed that in some years particles were transported almost completely out of the basin, whereas circulation in other years retained the majority of drifters within the seeding area (Bornholm Basin). A new retention index was derived that is associated to age 0 sprat recruitment in ICES Subdivision 25, estimated from area-disaggregated MSVPA runs. The significant linear relationship ($P<0.018$) between retention index and sprat recruitment explained 24% of the overall variability between 1979-2001. However, the correspondence has not been apparent during the 1980s, when both spawning stock biomasses and recruitment levels were consistently low in the central Baltic Sea. A strong positive coupling of recruitment success to basin retention was only seen during the last decade, characterized by relatively high levels of spawning stock biomass and a tremendous variability in sprat recruitment success. Retention indices corresponding to sprat larvae born late in the year (i.e. June) were much better correlated to recruitment success ($R^2 > 80\%$) than those derived from particles released earlier into the model domain. This intra-annual pattern may suggest that recruitment success in central Baltic sprat was – at least during the last decade - predominantly determined by the relative survival of larval cohorts emerging late in the spawning season. The index is significantly cross-correlated to other environmental time series, most importantly annual surface temperature in August, which makes it difficult to conclude on the processes crucial for central Baltic sprat recruitment success.

Introduction

The Baltic sprat, *Sprattus sprattus*, is presently the most abundant commercially exploited fish species in the Baltic Sea (ICES[1] 2004). Sustainable management is challenged by large fluctuations in stock size due to the combined effect of only few age-classes present in the population and a generally very variable recruitment success. Since spawning stock biomass is, at best, only a poor predictor of year-class strength in sprat (MacKenzie and Köster 2004), other biotic and abiotic variables must play a major role in determining the annual number of surviving recruits. For example, ambient temperature has been shown to influence both egg mortality (Köster et al. 2003b) and gonadal maturation (MacKenzie and Köster 2004) with significant consequences for sprat recruitment variability. The likely impacts of trends in predation pressure due to the decreased Baltic cod stock (Bagge and Thurow 1994) and/or shifts in zooplankton abundance on sprat recruitment have yet to be assessed.

Variability in ocean circulation leading to spatio-temporal differences in larval transport may also affect recruitment success, because physical forcing can cause retention or advection to areas suitable or unsuitable for larval survival (e.g. Werner et al. 1996, Heath and Gallego 1998). Following this rationale, Köster et al. (2003b) developed a "larval transport index" for sprat from the Bornholm Basin, being one of the main spawning grounds in the central Baltic Sea. The authors defined the index as the cumulative wind energy (W/m^2) within a 45 day period after average peak spawning of sprat, and assumed that indices above or below a given threshold be indicative of larval retention or dispersion. The specific thresholds were estimated from hydrodynamic modelling under constant wind forcing (Hinrichsen et al. 2001). When implemented into sprat recruitment models, however, the index failed to explain a significant amount of the overall recruitment variability in ICES Sub-division 25 (Köster et al. 2003b).

Instead of using cumulative wind energy as a proxy for larval retention/dispersion, an alternative approach would be to model larval drift directly by means of Lagrangian particle tracking. The method depends on realistic hydrodynamic circulation models that provide the opportunity to follow the fate of passive particles tracked backward or forward in time through the model domain. Lagrangian drift studies are useful to address questions on different spatial and temporal scales, ranging from identification of spawning and nursery grounds (e.g. Hinckley et al. 2001, Hinrichsen et al. 2003), coupled bio-physical IBM's (Werner et al. 1996, Brickman et al. 2001, Hinrichsen et al.

[1] International Council for the Exploration of the Sea

2002), to reconstruction of daily environmental histories at the level of the individual fish (e.g. Baumann et al. 2003).

Here we did not focus on individual particle trajectories, but rather on inter-annual differences in larval drift patterns on the spatial scale of the entire central Baltic Sea. A time-series of 24 years (1979-2001) of available forcing data was used as input to a hydrodynamic model, which has been shown reliable means to reproduce the circulation features in the Baltic Sea (Lehmann 1995, Lehmann and Hinrichsen 2000). Instead of considering only the time of peak spawning (e.g. May, MacKenzie and Köster 2004), we released several cohorts of drifters from April to July each year to encompass the whole average spawning season of sprat in the Central Baltic (Köster and Möllmann 2000). The results of this modelling exercise were first used to determine whether notable differences in retention/dispersion of particles indeed existed between years. If so, are these differences associated to sprat recruitment success and may therefore explain some of its inter-annual variability?

Material and Methods

The applied 3-dimensional, baroclinic circulation model is based upon a free surface Bryan-Cox-Semtner model (Killworth et al. 1991) adapted to the Baltic Sea as described in detail by Lehmann (1995) and Lehmann and Hinrichsen (2000). The model domain encompasses the entire Baltic Sea including the Gulf of Bothnia, Gulf of Riga, the Belt Seas, Kattegat, and the Skagerrak with a realistic bottom topography. The horizontal resolution is 5 km, a value corresponding to approximately half the internal Rossby radius in the Baltic Sea (Fennel 1991) that is necessary to fully resolve mesoscale motions (e.g. eddies). 60 vertical levels are specified with a thickness chosen to best represent the different sill depths in the Baltic Sea. The model is forced by actual meteorological data that were available at the Swedish Meteorological and Hydrological Institute (SMHI, Norrköping) for a time-series of 24 years (1979-2002). Simulated 3-dimensional velocity fields extracted from the circulation model were then used to derive Lagrangian drift routes of passive particles seeded into the model domain.

The release scheme of particles followed our intention to simulate the transport of feeding sprat larvae during an average spawning season for each of the 24 years in the central Baltic Sea. To facilitate later comparisons with recruitment data, we considered the model domain of the central Baltic represented by ICES Sub-division 25 (SD 25, Fig.1). Initial horizontal drifter positions were derived from average sprat egg

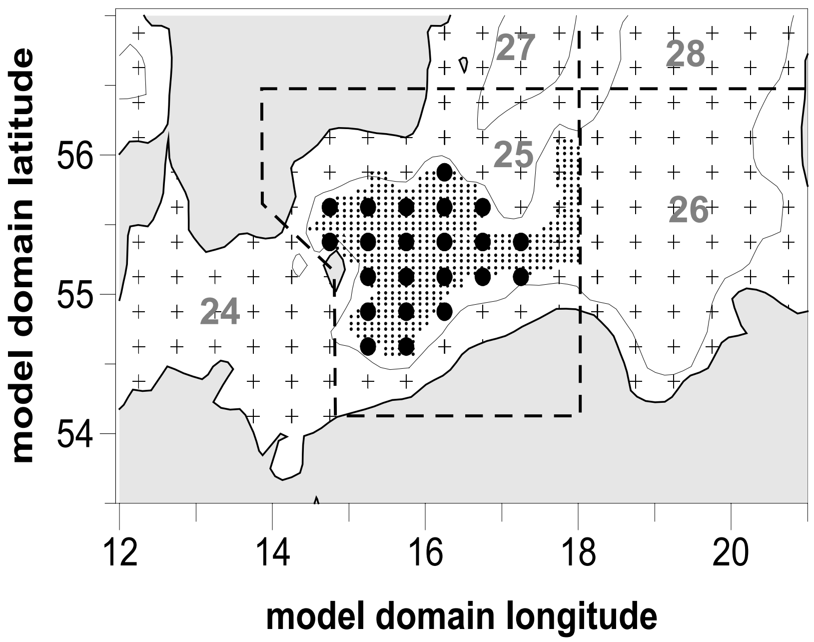

Fig.1: Section of the model domain showing the central Baltic Sea with 40 m depth contours and ICES Sub-divisions 24-28 (dashed lines). Small black dots depict seeding positions of Lagrangian drifters (5-10 m depth) that were released within SD 25. Big black dots and crosses refer to the midpoints of those 15x15 nm rectangles that were defined as retention and dispersion areas, respectively.

distributions in SD 25 (Köster 1994), assumed to be a proxy for the spatial distribution of first feeding sprat larvae. The vast majority of particles was thus released inside the 40 m isobath of the Bornholm Basin (Fig.1). All drifters were seeded and forced to remain within the 5-10 m depth layer, based on the assumption that feeding sprat larvae are found in surface waters and do not migrate vertically (STORE 2003). To test for this assumption, a second data set was derived by assigning to particles a simplified vertical migration pattern (0.5 d 5-10 m, 0.5 d 30-40 m). In both cases, batches of first feeding, passively drifting sprat larvae were released into the drift model on 21 April (day 111) and then every 10 days until 10 July (day 191). Each of these 9 larval ‘pulses’ per year consisted of 620 particles that were seeded in regular spatial intervals of about 5 km (Fig.1).

Depending on the seeding date, drifters were tracked through the model domain for a period of 36-116 days, until all positions were finally recorded on 15 August (day 227). This arbitrary date was chosen to compromise sufficient drift times for the ‘youngest particles’ (late release dates) whilst avoiding too long drift periods for the ‘oldest particles’ (early release dates). Because we were interested in broad scale patterns of particle distributions, a relatively coarse grid of 15x15 nm rectangles was devised (Fig.1) and the particles retained within each rectangle were counted. In a second step, all rectangles with midpoints located inside the 40 m isobath of the Bornholm Basin were defined as "retention area", whereas all other rectangles were defined as "dispersion area" (Fig.1). Lastly, the retention index was defined as the ratio of particles in the retention area to particles in the dispersion area.

A cumulative retention index was calculated encompassing the entire average spawning season, i.e. particles from all 9 release dates were collected together on 15 August and used to estimate the proportion retained in the Bornholm Basin. In a second analysis, 9 different retention indices were derived by considering each of the 9 release dates separately. These indices will hereafter be referred to as day specific retention indices.

Recruitment data of age 0 sprat in SD 25 were obtained from spatially dis-aggregated (i.e. separate for every sub-division), multi-species virtual population analyses (MSVPA) conducted by the ICES Baltic Fisheries Assessment Working Group for the years 1979-1999 (Appendix 1, Köster et al. 2001). We extrapolated recruitment data for 2000 and 2001 based upon sprat recruitment in the entire Baltic Sea (standard assessment, ICES 2003) and the average proportion of SD 25 recruits to the rest of the Baltic Sub-divisions (1995-1998). To allow for comparisons with recruitment models published before (Köster et al. 2003b), the time-series of spawning stock biomass (SSB) in SD 25 was updated in the same way, while mid-water and surface temperatures in SD 25 were retrieved directly from the ICES oceanographic database (Appendix 1).

As in Koester et al. (2003b), linear regression analyses were used to reveal potential relationships between retention indices and age 0 sprat recruitment in SD 25, whereas the influence of multiple factors (e.g. SSB or temperature) on sprat recruitment success was studied by multiple linear regressions. Durban-Watson statistics were used (SPSS 10.0) to assess the level of autocorrelation within each time-series.

Results

Drift patterns and final particle distributions were similar for the two data sets modelling larval sprat advection with and without vertical migration. However, a consistently better correspondence to sprat recruitment was found when vertical migration was not included, the results below are therefore restricted to simulations of particles constrained to the surface layer (5-10 m).

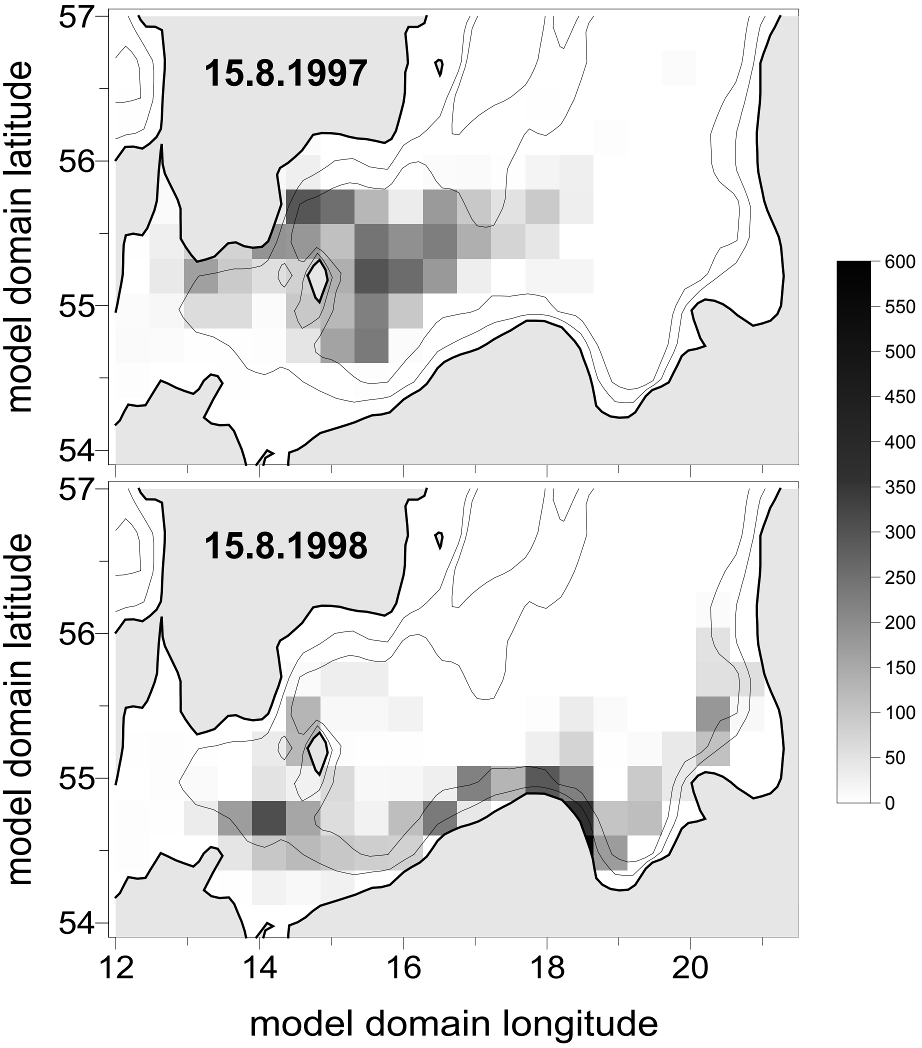

Fig.2: Examples of two contrasting outputs of particle drift simulations for years 1997 (retention year) and 1998 (dispersion year). Shading corresponds to the number of particles collected on 15 August (day 227) each year in each 15x15 nm rectangle. 20 m and 40 m depth contours are shown.

Model outputs showed remarkable inter-annual differences in the number of particles retained within the Bornholm Basin, allowing for a relatively clear division into either predominant retention or dispersion years. For example, final particle distributions for 1997 suggested an almost ideal retention situation, whereas in 1998 the majority of drifters were transported out of the basin (Fig.2). In dispersion years, most particles were found in rectangles south and south-east of the Bornholm Basin (60%) with notable numbers ending in western and inner parts of the Gdansk Bay (Fig.2). West- or northward advection was of minor importance.

Reflecting these patterns, the time-series of the cumulative retention index showed a high variability between successive years, in particular during the last decade (Fig.3). Between 1993-2001, the retention index corresponded well to recruitment success of

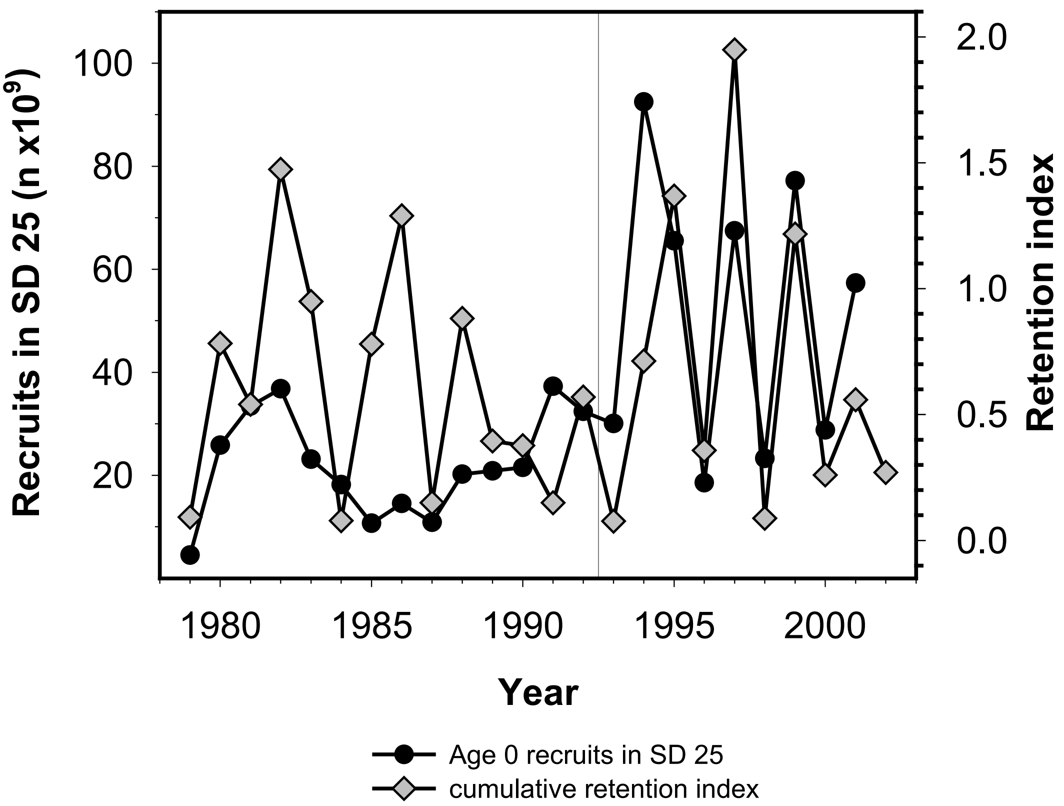

Fig.3: Time-series of recruitment success of age 0 sprat in SD 25 and the cumulative retention index, calculated from long-term Lagrangian drift simulations in the Baltic Sea (1979-2002). High indices are indicative of strong retention situations in the Bornholm Basin, whereas low values point towards years of predominant dispersion of drifters out of the basin.

age 0 sprat in SD 25, indicating that years of strong particle retention coincided with high sprat recruitment, whereas dispersion years were associated with low recruitment success (Fig.3). By including all years of available data (1979-2001), the significant (P=0.018) linear relationship between sprat recruitment and retention index explained 24% of the overall variability (Fig.4). However, excluding the last nine years of data (1993-2001) obliterated the relationship and confirmed that a strong coupling between retention and recruitment only occurred during the past decade (Fig.4). This can also be inferred from Fig.5, where R^2-values for the 16 different subsets of time-series data (1979/1993-2001) suggest an increase of explained variability in the linear recruitment-retention regressions during the late 1980s. Since the beginning of the 1990s, the cumulative retention index alone explained close to 50% of recruitment variability in central Baltic sprat (Fig.5).

Day specific retention indices were all significantly correlated to sprat recruitment success (1979-2001, P_{min}/P_{max}=<0.001/0.028), however, the amount of variability explained by the linear regressions increased with the day of release (Fig.6). While each

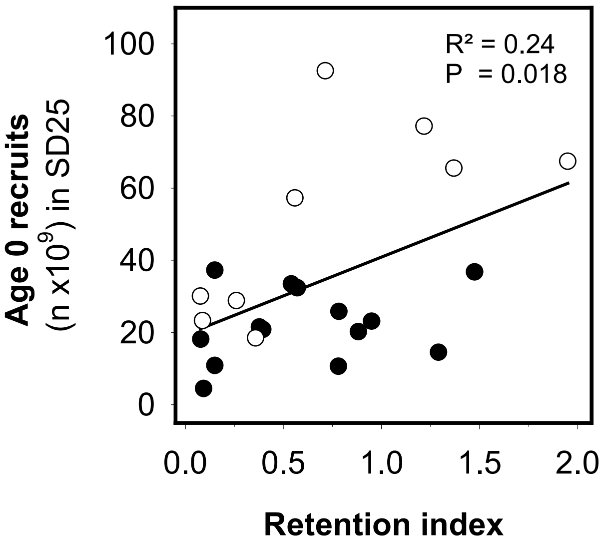

Fig.4: Relationship between recruitment success of age 0 sprat in SD 25 and cumulative retention index, using all 23 years of available recruitment data from MSVPA. Filled circles refer to years 1979-1992, empty circles to 1993-2001.

of the early seeding days (d111-d151, corresponding to 116-76 days of particle tracking) only explained about 22% of recruitment variability between 1979-2001, the specific retention index for day 181 (46 days of particle tracking) had an explanatory power of 54% (Fig.6).

If both effects, i.e. release day and length of the sprat recruitment time-series, were combined, the corresponding R^2-values of the recruitment-retention relationships increased considerably with late release days and shorter time-series (Fig.7). For example, during the past decade (1990-2001), retention indices derived from release day 181 were very strongly correlated to sprat recruitment success in SD 25, explaining more than 80% of the overall variability.

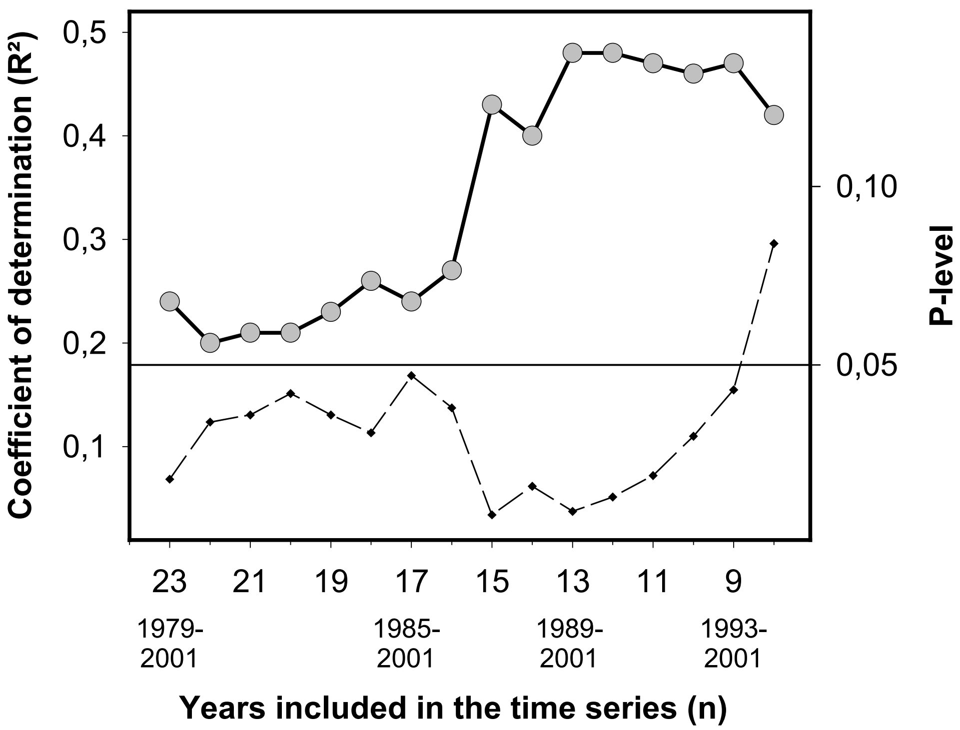

Fig.5: Amount of variability (R^2) explained by linear regressions of age 0 sprat recruitment in SD 25 on cumulative retention index using different subsets of the available time-series (MSVPA) data. The data sets were generated by successively excluding the respective earliest year in the time-series. The dashed line shows corresponding P-values for each of the 16 regressions.

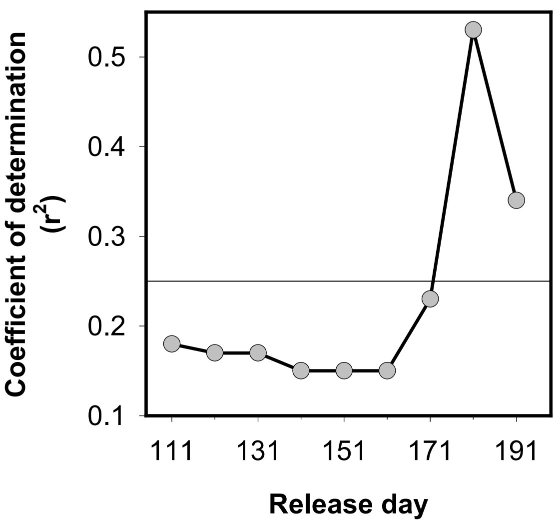

Fig.6: Effect of particle release day on the amount of variability (R^2-value) explained by linear regressions of sprat recruitment (1979-2001) on day specific retention index. The thin black line refers to the R^2-value of the linear regression using the cumulative retention index as the independent variable.

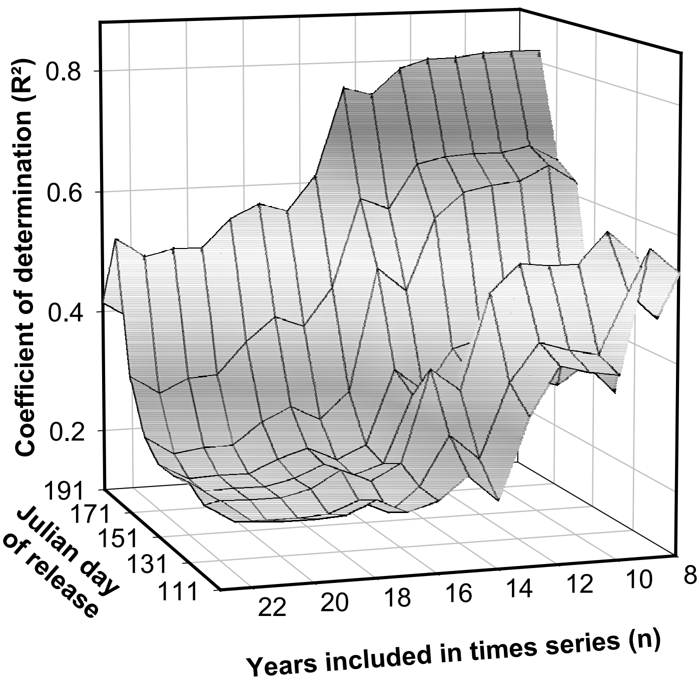

Fig.7: Surface plot showing the combined effect of release day and length of the recruitment data time-series on the amount of explained variability (R^2) in the linear regressions of age 0 sprat recruitment on the retention index.

Inclusion of the retention index improved the sprat recruitment model of Koester et al. (2003), which used spawning stock biomass and mid-water (40-60 m) temperature in May in SD 25 as independent variables in a multiple linear regression (Table 1, Model I). By adding the cumulative retention index (Model II) or the specific retention index for day 181 (Model III) as a third independent variable, the amount of explained variability increased from 45% to 58% or 72%, respectively.

Table1: Multiple linear regressions of age 0 sprat recruitment in SD 25 on SSB (t), winter-water temperature in May in SD 25 (°C), and retention index: parameter estimates and their significance level.

	Model I	Model II	Model III
dependent variable	Ln (age 0 recruits in SD25)	Ln (age 0 recruits in SD25)	Ln (age 0 recruits in SD25)
years incl	1979-2001	1979-2001	1979-2001
P	0.003	0.001	<0.001
R^2	0.448	0.584	0.723
Durbin-Watson	1.898	1.782	1.756

included variables	**P**	**B**	**included variables**	**P**	**B**	**included variables**	**P**	**B**
Constant	<0.001	22.69	Constant	<0.001	22.466	Constant	<0.001	22.323
SSB	0.032	2.25E-06	SSB	0.032	2.02E-06	SSB	0.43	1.57E-06
Temperature	0.011	0.244	Temperature	0.009	0.226	Temperature	0.002	0.225
			cumulative retention index	0.022	0.505	specific retention index d181	<0.001	0.818

Discussion

Our attempt to quantify inter-annual differences in modelled drift patterns of larval sprat has led to the definition of a new index of retention/dispersion for the central Baltic Sea. We compared the index` annual fluctuations with the time series of age 0 sprat recruitment in SD 25 and found that the degree of correspondence between retention and recruitment shifted markedly from very low values throughout the 1980s to strong coupling during the past decade. The significant, positive relationship indicated that poor sprat recruitment occurred predominantly in years of strong advection out of the Bornholm Basin towards the southern coast. Conversely, above-average sprat recruitment was seen in years of relative particle retention.

Inferences like these that are drawn from Lagrangian simulations rely on the assumption that trajectories of passive particles are representative of the average drift of the planktonic species or life-stage studied. In demersal fish like cod or flatfish, juvenile settlement concludes the susceptibility to ocean circulation and thus sets a natural limit to drift studies (e.g. 65 days, Hinrichsen et al. 2003). Such a limit, however, is not as readily defined in pelagic species like sprat. The onset of active swimming behaviour or schooling may not necessarily preclude Lagrangian drift studies, if late-larvae or early juveniles keep moving randomly within a water body that is subject to predictable physical forcing. In the Baltic Sea, for example, non-indigenous species such as juvenile whiting (*Merlangius merlangus*), horse mackerel (*Trachurus trachurus*), or anchovy (*Engraulis encrasicolus*) are frequently observed after major intrusions of North Sea water into the Baltic proper. For adult horse mackerel, a link could be established between migration patterns in the north-eastern North Sea and changes in the Atlantic inflow (Iversen et al. 2002). For juvenile sprat, it may thus be justified to assume an average drift not against but along the major flow fields as derived from the circulation model. This is supported by our results showing no conflicting particle distributions between different seeding days, i.e. our decision upon retention or dispersion in a given year was not affected by the length of the drift period. All day specific retention indices were significantly correlated to sprat recruitment strength, although those of early released drifters explained only a small fraction of the overall variability. This may partly be because the level of uncertainty generally increases with the length of the particle simulation.

The retention-recruitment relationship suggested that years of strong larval/juvenile dispersion from the Bornholm Basin resulted in increased mortality and therefore relative recruitment failure in SD 25. Alternatively, it could be possible that displaced cohorts survived and simply recruited into one of the neighbouring Baltic sub-divisions. The potential for large-scale, eastward transport of sprat larvae has already been described by Grauman (1976) and was also noticed in our particle distributions during

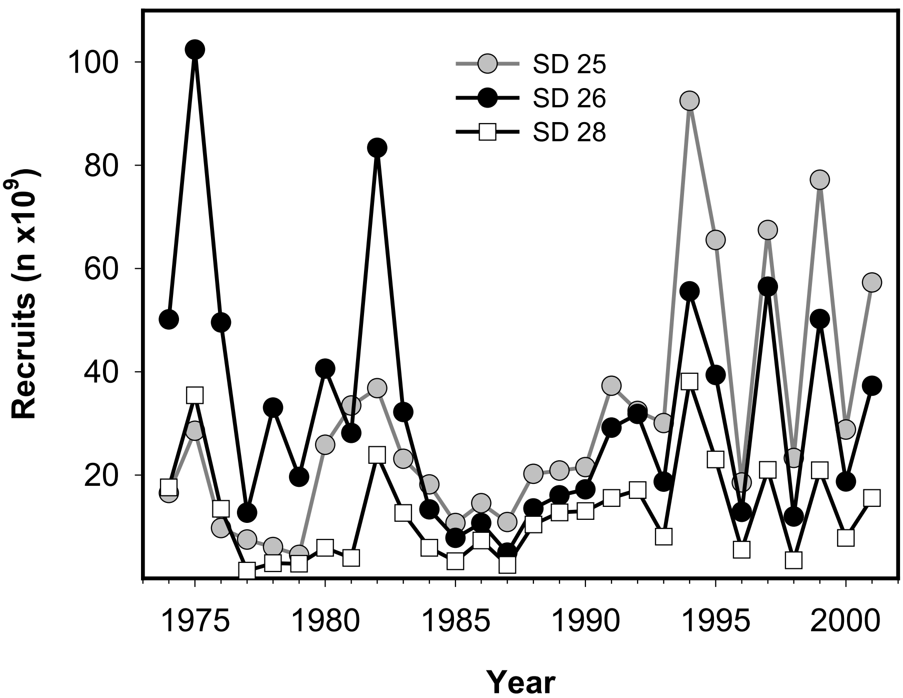

Fig.8: Recruitment success of age 0 sprat in Baltic sub-divisions 25, 26, and 28 (see Fig.1) between 1974-2001 as derived from MSVPA.

strong dispersion years. To address this concern, we compared recruitment success of age 0 sprat from SD 25 with SD 26 (Gdansk Bay) and SD 28 (Gotland Basin) for a time series of 28 years (1974-2001, Fig.8). The overall positive correlations between all sub-divisions, however, did not support the hypothesis of major proportions of SD 25 sprat drifting and recruiting into areas of the eastern Baltic Sea. We therefore concluded that a) particle distributions in the model reflected the major drift patterns of larval/juvenile sprat from the Bornholm Basin, and that b) the retention index was associated to genuine variability in pre-recruit sprat survival causing the observed recruitment variability in SD 25.

Coupling of recruitment success to advective processes has already been demonstrated in a number of species and for different marine systems, including the Baltic Sea. For Baltic cod larvae it was shown that retention *to* but also advection *out of* the central Bornholm Basin could have beneficial effects to survival, depending on the abundance of the calanoid copepod *Pseudocalanus elongatus* (Hinrichsen et al. 2002, 2003). Shackell et al. (1999) derived a "retention/survival-index" for haddock larvae hatched on the south-west Nova Scotian Shelf and inferred that surviving age 2 haddock were likely those that had been retained on the shelf. In the highly dynamic Benguela current off South Africa, recruitment success of anchovy larvae crucially depends on on-shore advection and retention, whereas major dispersion into the open ocean causes recruitment failure (Hutchings et al. 2002). In this study, we also observed low recruitment success corresponding to years of strong dispersion from the sprat spawning ground. In dispersion years, we further noticed a tendency for fewer particles being retained in a greater number of rectangles (e.g. Fig.2), a situation indicative of decreased spatial integrity in dispersed larval cohorts. This could result in higher encounter rates with potential predators (e.g. cod, adult herring) and therefore have adverse effects to recruitment; a concept consistent with Sinclair's (1988) member/vagrant hypothesis. However, there is still no coherent explanation, why exactly shallow, coastal waters (<20m) should be areas unfavourable for larval/juvenile survival. In contrast to the relative wealth of data available for the Bornholm Basin, data on the adjacent coastal areas are still relatively scarce. For example, if predation is considered one of the important mechanisms, the abundance of potential predators occurring in coastal waters during summer has to be investigated in more detail.

Variable physical forcing does not only cause variability in ocean circulation, but potentially also influences ambient temperature and prey abundance, which are key environmental factors affecting growth and survival in pre-recruit life stages (Heath 1992). The consequence of such interactions is that retention vs. dispersion, as inferred from particle drift simulations, may only be concomitant but not necessarily causal processes to recruitment strength. To test for potential cross-correlations between

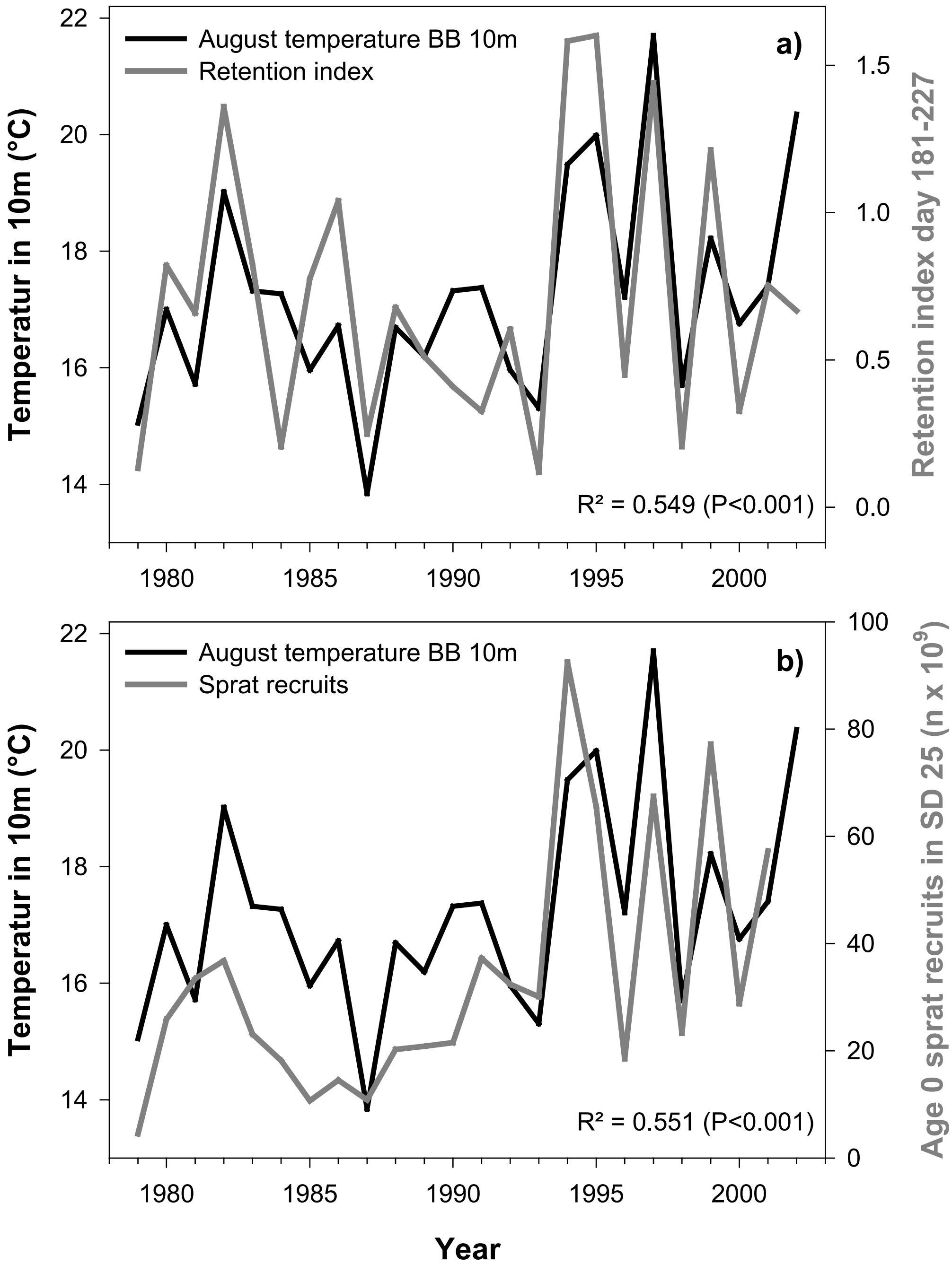

Fig.9: Correspondence between time-series of August surface temperature (10 m) in the Bornholm Basin and a) specific retention index for day 181 (30.June), and b) recruitment success of age 0 sprat in SD 25. Correlation coefficients (R^2) and P-values are given for linear regressions.

temperature, retention index and sprat recruitment, we obtained temperature data for SD 25 in 10 m depth, available at the ICES oceanographic database (Appendix 1). For each year (1979-2001) a monthly average temperature value was calculated between April and September. We found that sea surface temperature in July and August was significantly ($P<0.001$) correlated to both the cumulative and the specific retention index for day 181, explaining up to 55% of the overall variability (Fig.9a). Sea surface temperature also explained a significant proportion of sprat recruitment variability in SD 25 (Fig.9b), but only for months July (20%), August (55%) and September (22%). The positive relationship between sea surface temperature in summer and sprat recruitment could be interpreted in terms of lower cumulative mortalities of pre-recruit sprat due to accelerated growth and shorter stage durations (Pepin 1991).

Hinrichsen et al. (2001) published daily wind speeds and directions over the Bornholm Basin for 1993 and 1994, two years of markedly different sea surface temperatures and retention indices. While winds until May were similar between the two years, the authors found major differences in wind patterns during the summer months June-August. Combining both studies, we suggest that strong to variable *westerly* winds cause both cold surface temperatures in the Bornholm Basin and a high degree of larval dispersion towards the south-east (e.g. 1993), and are associated to relatively weak sprat recruitment in SD 25. Conversely, weak *easterly* winds seem conducive to warm surface temperatures and relative larval retention (e.g. 1994), a situation associated to sprat recruitment success.

At least during the last decade, surface temperature and drift data indicate that the late summer months July-August play a crucial role in determining the number of surviving age 0 sprat recruits in SD 25. This could be due to a shift in spawning time, which is not apparent from field measurements of seasonal sprat egg abundance in 1999 (STORE 2003) and in 2002 (Voss et al. 2004). An alternative explanation would be that sprat larvae born late in the year have a higher probability of survival than their earlier born conspecifics and therefore mainly determine the strength of recruitment. This hypothesis is corroborated by results from an otolith-based survivor analysis carried out in 2002 (Voss et al. 2004), suggesting a selective survival of summer (June) over spring born sprat (April) in SD 25. However, it should be noted that by August even sprat born at the end of the spawning season will likely be in the juvenile rather than still in the larval stage.

During the last two decades, a regime shift in the upper trophic level of the central Baltic Sea ecosystem has occurred from a cod-dominated to a sprat-dominated system (Köster et al. 2003a). Sprat spawning stock biomass has increased considerably during the past decade (Fig.10), and the pattern of sprat recruitment has shifted from consistently low to highly variable (ICES 2004, Fig.3). Concurrently, standing stocks of the copepod *Acartia* spp., a key component of larval sprat diet (Voss et al. 2003), have increased in the Baltic Sea since the late 1980s due to shifts in hydrographic conditions (Möllmann et al. 2000). Because sprat recruitment is not likely controlled by a single factor, changes in one variable (e.g. cod abundance) may have altered the relative importance of the other recruitment determinants (e.g. temperature, food, or retention). We suggest that this is why we observed a pronounced change in the recruitment-retention relationship, indicating that advective processes have shifted from apparently inconsequential during the 1980s to highly influential to sprat recruitment during the last decade.

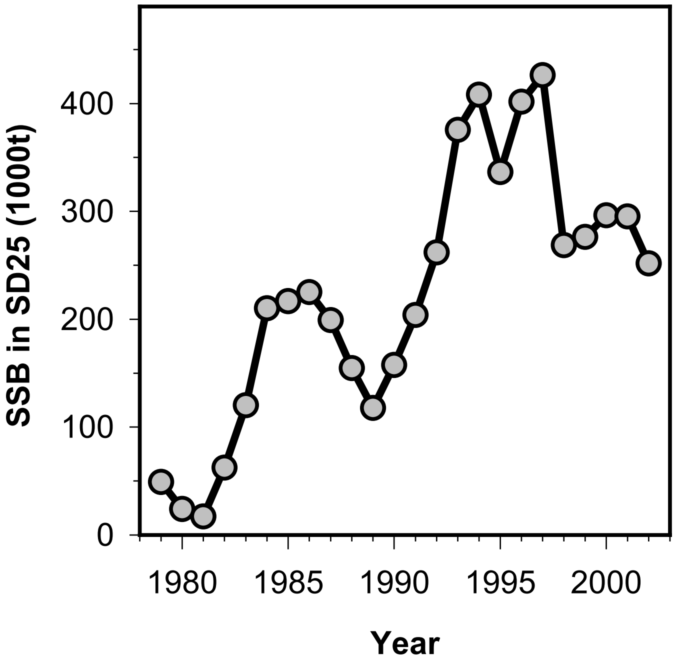

Fig.10: Spawning stock biomass (SSB) of sprat in SD 25 between 1979-2002.

In conclusion, this study advocates a dependency of sprat recruitment success on ocean circulation patterns resulting in retention to or dispersion from the major sprat spawning ground in the central Baltic Sea. It has also highlighted the persisting need to identify and disentangle the underlying mechanisms causing the observed relationships. Previous research effort has focused primarily on egg and early larval stages of sprat, and field campaigns have been restricted almost exclusively to the central areas of SD 25, i.e. the Bornholm Basin. Our results suggest that dispersion to very shallow coastal waters may be more important than previously acknowledged, and may draw attention to factors influencing growth and survival in later developmental stages (i.e. late larvae, early juveniles) of Baltic sprat.

Acknowledgements

This study was funded by the GLOBEC-Germany project (FKZ 03F0320E). We like to thank Christian Möllmann for stimulating comments and discussions.

References

Bagge, O., and Thurow, F. 1994. The Baltic cod stock: fluctuations and possible causes. ICES Mar. Sci. Symp. 198:254–268.

Baumann, H., Pepin, P., Davidson, F.J.M., Mowbray, F., Schnack, D., and Dower, J.F. 2003. Reconstruction of environmental histories to investigate patterns of larval radiated shanny (*Ulvaria subbifurcata*) growth and selective survival in a large bay of Newfoundland. ICES Journal of Marine Science 60:243-258

Brickman, D. Shackell, N.K., Frank, K.T 2001. Modelling the retention and survival of Browns Bank haddock larvae using an early life stage model. Fisheries Oceanography 10: 284-296

Fennel, W. 1991. Rossby radii and phase speeds in the Baltic Sea. Continental Shelf Research 11:23-36

Grauman, G.B. 1976. On the distribution and passive migration of Baltic sprat eggs and larvae in Bornholm-Slupsk spawning ground. ICES CM 1976/P:8

Heath, M. R. 1992. Field investigations of the early life stages of marine fish. Advances in Marine Biology 28:1-174

Heath, M. and Gallego, A. 1998. Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. Fisheries Oceanography 7:110-125

Hinckley, S., Herrman, A.J., Meir, K.L., Megrey, B.A. 2001. Importance of spawning location and timing tom successful transport to nursery areas: a simulation study of Gulf of Alaska walleye pollack. ICES Journal of Marine Science 58: 1042-1052.

Hinrichsen, H.-H., St. John, M.A., Aro, E., Grønkjær, P., and Voss, R. 2001. Testing the larval drift hypothesis in the Baltic Sea: retention vs. dispersion due to the influence of wind driven circulation. ICES Journal of Marine Science 58 :973-984

Hinrichsen, H.-H., Möllmann, C., Voss, R., Köster, F.W., and Kornilovs, G. 2002. Biophysical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59:1858-1873

Hinrichsen, H.-H., Lehmann, A., Möllmann, C., and Schmidt, J. O. 2003. Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography 12:425-433

Hutchings, L., Beckley, L.E, Griffiths, M.H., Sundby, S., and van der Lingen, C. 2002. Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. Journal of Marine and Freshwater Research 53:307-318

ICES. 2003. Report of the Baltic Fisheries Assessment Working Group. ICES CM 2003/ACFM:21

ICES. 2004. Report of the Baltic Fisheries Assessment Working Group. ICES CM 2004/ACFM:22

Iversen, S.A., Skogen, M.D., and Svendsen, E. 2002. Availability of horse mackerel (*Trachurus trachurus*) in the north-eastern North Sea, predicted by the transport of Atlantic water. Fisheries Oceanography 11:245-250

Killworth, P.D., Stainforth, D., Webbs, D.J., and Paterson, S.M. 1991. The development of a free-surface Bryan-Cox-Semtner ocean model. Journal of Physical Oceanography 21:1333-1348

Köster, F.W. (1994). Der Einfluß von Bruträubern auf die Sterblichkeit früher Jugendstadien des Dorsches (*Gadus morhua*) und der Sprotte (*Sprattus sprattus*) in der zentralen Ostsee. Berichte aus dem Institut für Meereskunde Kiel 261: 286pp

Köster, F.W., and Möllmann, C. 2000. Egg cannibalism in Baltic sprat *Sprattus sprattus*. Marine Ecology Progress Series 196:269-277

Köster, F.W., Möllmann, C., Neuenfeldt, S., St. John, M.A., Plikshs, M., and Voss, R. 2001. Developing Baltic cod recruitment models. I. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring, and sprat. Canadian Journal of Fisheries and Aquatic Sciences 58:1516-1533

Köster, F.W., Möllmann, C., Neuenfeldt, S., Vinther, M., St. John, M.A., Tomkiewicz, J., Voss, R., Hinrichsen, H.H., Kraus, G., Schnack, D., 2003a. Fish stock development in the Central Baltic Sea (1976-2000) in relation to variability in the environment. ICES Mar. Sci. Symp., 219:294-306

Köster, F.K., Hinrichsen, H.-H., Schnack, D., St.John, M.A., MacKenzie, B.R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., and Aro, E. 2003b. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. Scientia Marina 67 (Suppl.1): 129-154

Lehmann, A. 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus, 47A:1013-1031

Lehmann, A., and Hinrichsen, H.-H. 2000. On the thermohaline variability of the Baltic Sea. Journal of Marine Systems 25:333-357

MacKenzie, B., and Köster, F.W. 2004. Fish production and climate: sprat in the Baltic Sea. Ecology 85:784-794

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences 48:503-518

Shackell, N.L., Frank, K.T., Petrie, B., Brickman, D., and Shore, J. 1999. Dispersal of early life stage haddock *Melanogrammus aeglefinus* as inferred from the spatial distribution and variability in length-at-age of juveniles. Canadian Journal of Fisheries and Aquatic Sciences 56:1-12

Sinclair, M. 1988. Marine populations: an essay on population regulation and specification. University of Washington Press, Seattle, USA

STORE, 2003. Environmental and fisheries influences on fish stock recruitment in the Baltic Sea. Final Consolidated Report to the EU Commission, FAIR 98 3959 Part 1 & 2. European Commission, Directorate General XIV Fisheries, rue de la Loi 200, 1049 Brussels, Belgium.

Voss, R., Köster, F.W., and Dickmann, M. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research 63:97-111

Voss, R., Clemmesen, C., Baumann, H., and Dickmann, M. 2004. Recruitment success in Baltic sprat: Coupling of food availability, larval condition and survival. ICES CM 2004/O:02

Werner, F.E., Perry, R.I., Lough, R.G., Naimie, C.E. 1996. Trophodynamics and advective influences on Georges Bank larval cod and haddock. Deep-Sea Res. II, 43: 1793-1822.

Appendix

	cumulative retention index	specific retention index d181	SSB SD25 (t)	Temperature (°C) May 45-65 m	Temperature (°C) August 10 m	recruits age 0 SD 25
1979	0.093	0.132	49053	1.47	15.05	4486577000
1980	0.783	0.821	23975	2.62	17	25831940000
1981	0.541	0.659	17023	2.59	15.72	33438650000
1982	1.474	1.359	62236	3.04	19.02	36793030000
1983	0.949	0.825	120016	4.08	17.32	23120710000
1984	0.079	0.205	209986	2.89	17.27	18154790000
1985	0.78	0.775	216565	0.75	15.96	10668480000
1986	1.29	1.040	225051	2	16.72	14510420000
1987	0.15	0.248	198961	1.04	13.84	10845030000
1988	0.882	0.678	154521	4.07	16.69	20217650000
1989	0.395	0.511	117614	4.99	16.19	20854610000
1990	0.377	0.409	157467	5.7	17.32	21509500000
1991	0.15	0.325	203886	3.53	17.37	37266210000
1992	0.57	0.603	261841	3.99	15.96	32375230000
1993	0.077	0.118	375485	4.29	15.3	30058910000
1994	0.713	1.582	408172	3.18	19.49	92479960000
1995	1.368	1.601	336219	4.68	19.99	65517750000
1996	0.358	0.449	401502	1.18	17.21	18520080000
1997	1.949	1.440	426282	4.47	21.7	67448180000
1998	0.088	0.206	268555	4.55	15.7	23271810000
1999	1.217	1.212	276268	4.09	18.22	77155826394
2000	0.26	0.325	296374	4.84	16.76	28793231332
2001	0.559	0.753	295180	4.06	17.4	57291136305